The Dynamic Equations of the Tree Morphogenesis GreenLab Model

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Thème 4 — Simulation et optimisation
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Abstract: We explicit the dynamic equations followed by a tree during its growth according to the Greenlab model. In a first part we explicit the Organogenesis equations. In the second part, we recall the equations which, using a macroscopic photosynthesis point of view, describe with a great precision the evolution of the organ sizes. In a third part we establish the morphogenesis equations describing the geometry of a tree. The three parts are illustrated with an example.

Key-words: GreenLab, Plant Morphogenesis, Tree Architecture

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La dynamique du modèle GreenLab de la morphogénèse des arbres

Résumé : On explicite les équations suivies par la dynamique des plantes lors de leurs croissances selon le modèle GreenLab. Dans une première partie on donne les équations vérifiées par l'organogénèse. Dans une deuxième partie, on rappelle les équations qui, utilisant un point de vue macroscopique de la photosynthèse, décrivent avec une grande précision l'évolution de la taille des organes. Dans la troisième partie on établit les équations de la morphogénèse décrivant la géométrie de la plante. Les trois parties sont illustrées sur un exemple.

Mots-clés : GreeLab, Morphogénèse des plantes, Architecture des plantes

1 Introduction

Mathematical models on tree architecture principally concern the step by step algorithms depending on a genetic program, that insure the organ poduction during the growth process. Adding geometrical rules, one can obtain nice shapes of trees that are used mainly in the world of computer graphics. This pure morphogenetic approach has given more particularly a formalism based on grammar called L-System [11] or on Automata [14].

In Agronomy, the vegetable matter production is the main goal. Simulation of the photosynthesis (biomass production and biomass allocation) is then performed, thank to crude plant models mainly divided in compartments (leaves, branches, roots,...). No specific formalism has been developed in these last cases [2, 12].

Recently a new kind of tree models arouse, named "structural functional tree" [9, 13, 6]. These models endeavour to combine both aspects : organogenesis and photosynthesis. The L-System approach has, then, also incorporated interactions with environment[10, 8]. In all the cases the principle of the growth starting from seed and the parallel simulation of numerous buds can make the computing time of a big tree quite long.

A new approach of tree computation has been done in the dynamical model GreenLab. Thanks to the Physiological Age notion and the botanical description, it is possible to divide a tree according to substructures that can be retrieved frequently inside the main architecture. Computing only one time these substructures improves dramatically the speed of the computation [3, 4, 5]. Here we explicit the delay equations describing the tree dynamics used in GreenLab software which contains by construction this factorization.

2 Organogenesis

2.1 Introduction

Buds construct axis by setting in place *Growth Unit* rhythmically. Each Growth Unit is composed of one or several *metamers* of different kinds, that are sets of internodes, axillary buds, leaves and fruits. In parallel the axillary buds give birth to secondary branches that have same kind of organization as the main axis.

Usually the number of different types of axis in a tree is limited. These types are related to *Physiological Age* [1]. It is seldom more than six. A same kind of axis can be found everywhere in the tree architecture and it is not necessarily linked to the branching order.

Even an axis can be composite because the apical bud can change of Physiological Age during the growth process. So the tree looks as a stack of lateral and terminal substructures, showing a multiscale organisation that in some particular cases gives a fractal shape.

Even each substructure can be always divided into a Bearing Axis and lateral and terminal substructures. The main structure is called the *architectural unit* in Botany. Repetition of this structure when the tree gets aged is called *reiteration*, meanwhile the branches are substructures that can easily be identified according to their Physiological Ages .

2.2 Tree Organogenesis

More precisely the tree organisation has four levels of ascending scales : – metamer, – Growth Unit , – Bearing Axis , – substructure.

• Any metamer $m_{pq}(k,n)$ of a tree can be identified thank to 4 indices.

1. The Chronological Age of the tree n.
2. The Physiological Age $p \in \mathcal{P} = \{1, \cdots, P\}$ of the Growth Unit and Bearing Axis it belongs.
3. The Physiological Age q of the substructures branched on it. Normally the axillary bud has a Physiological Age older than the bearing internode. If it is equal, the substructure is named *reiteration*. On trees, the common way to organize the bud series, along a Growth Unit of Physiological Age p, is to start from p at the tip and to end with the oldest Physiological Age of the plant. This hierarchical order is named *acrotony* in Botany.
4. The Chronological Age k of the metamer that bears the organ.

The index n is necessary because the organ sizes of same Chronological Age and Physiological Age change with the plant age. A metamer bears several organs (identified by the indices o) that are : – internodes (denoted by e), – leaves (denoted by a), – fruits, – rings. The numbers of these organs are denoted $m^o_{pq}(k,n)$.

• The Growth Unit is composed of metamers m_{pq} repeated r_{pq} times with b_{pq} axillary buds[1]

• The concatenation of the Growth Units of the different Physiological Ages (called $R_p(k,n,S)$) and the final bud defines the Bearing Axis . After τ_p repetitions the final bud of the Bearing Axis (of Physiological Age p) can mute or die. The mutation gives birth to another terminal substructure of Physiological Age $\mu(p)$ older than p.

• A substructure of Physiological Age p, Chronological Age k on a tree of age n is called $S_p(k,n)$. It is the set of all the metamers stacked on its Bearing Axis and its lateral substructures. And therefore the complete tree of Chronological Age n is $S_1(n,n)$. A bud of Physiological Age p on a tree of age n is the substructure $S_p(0,n)$ is independent of n and denoted s_p (seed of Physiological Age p substructures).

The substructure $S_p(k,n)$ is seen, at mathematical level, as a word when the alphabet is the set of metamers $\Sigma = \{m_{pq}(k,n) \mid p,q \in \mathcal{P}\}$. The set of words endowed with the concatenation seen as an internal operation is denoted Σ^*.

When we are not concerned with the size of the organs $m_{pq}(k,n) = m_{pq}$ and we have $S_p(k,n) = S_p(k,k)$ for all $n \geq k$.

In the following we will write $S_p(k)$ for $S_p(k,n)$, even when $m_{pq}(k,n)$ is not constant in k and n, because in this case the index n is common to all the terms. The dynamic of the substructure is given by :

[1] Usually a leaf is associated to axillary buds.

$$S_p(0) = s_p \ , \tag{1}$$
$$S_p(k) = R_p(k,S)S_p(k-1) \ , \qquad 0 < k < \tau_p \ , \tag{2}$$
$$S_p(k) = T_p(k,S)S_{\mu(p)}(k-\tau_p) \ , \qquad \forall k \geq \tau_p \ , \tag{3}$$

with

$$R_p(k,S) = \prod_{q>p} \left\{ m_{pq}(k) S_q(k-1)^{b_{pq}} \right\}^{r_{pq}} \ , \tag{4}$$

$$T_p(k,S) = \prod_{l=k-\tau_p+1}^{k} R_p(l,S) \ . \tag{5}$$

2.3 Example

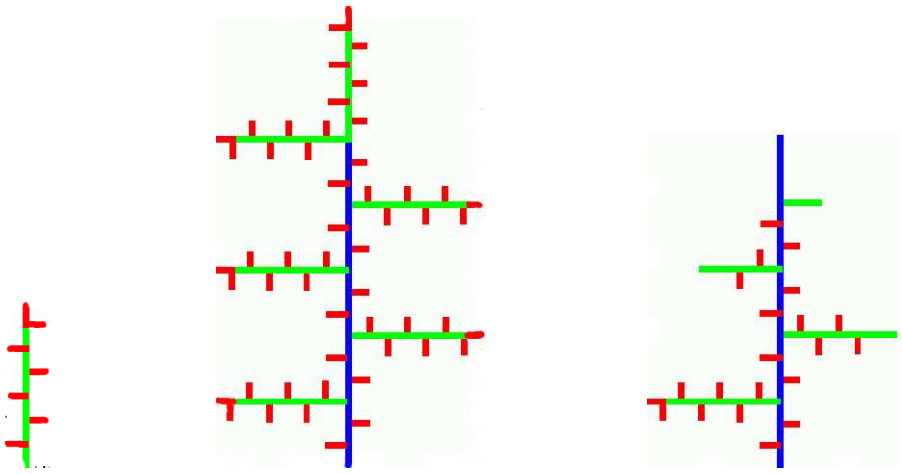

Figure 1: $S_2(4)$, $S_1(9)$ and the tree at age 5.

Let us consider the tree given in Figure 1. It has three ($P = 3$) Physiological Ages represented by the different colors (the blue corresponds to 1, the green to 2, the red to 3). After 9 cycles ($n = 9$) the tree is complete, that is no new organs can be created, $b_{pq} = 1$ for all p and q, $r_{13} = 2$, $r_{12} = 1$, $r_{23} = 2$, $\tau_1 = 5$, $\tau_2 = 3$, $\tau_3 = 1$, $\mu(1) = 2$, $\mu(2) = 3$, $\mu(3) = \bullet$ where "$\bullet$" denotes the death.

Supposing that the metamers m_{pq} do not depend on k and n we can specialize the dynamic equations.

$$
\begin{aligned}
&S_p(0) = s_p \ , && 1 \le p \le 3 \ , \\
&S_3(k) = m_{3\bullet} \ , && \forall k \ge 1 \ , \\
&S_2(k) = \{m_{23} S_3(k-1)\}^2 S_2(k-1) \ , && 0 < k < 3 \ , \\
&S_2(k) = \prod_{l=k-3}^{k-1} \{m_{23} S_3(l)\}^2 S_3(k-3) \ , && \forall k \ge 3 \ , \\
&S_1(k) = \{m_{13} S_3(k-1)\}^2 m_{12} S_2(k-1) S_1(k-1) \ , && 0 < k < 5 \ , \\
&S_1(k) = \prod_{l=k-5}^{k-1} \left\{\{m_{13} S_3(l)\}^2 m_{12} S_2(l)\right\} S_2(k-5) \ , && \forall k \ge 5 \ .
\end{aligned}
$$

Then the red stick is $m_{3\bullet}$ where the dot is for Physiological Age corresponding to the death (a dead bud). It corresponds to the complete substructure of Physiological Age 3.

The complete substructure of Physiological Age 2 is given in Figure 1. It is

$$S_2(4) = (m_{23} m_{3\bullet})^6 m_{3\bullet} \ .$$

We see that it appears 6 times in the complete tree. The complete tree appears at age 9 with formula

$$S_1(9) = \{(m_{13} m_{3\bullet})^2 m_{12} (m_{23} m_{3\bullet})^6 m_{3\bullet}\}^5 (m_{23} m_{3\bullet})^6 m_{3\bullet} \ .$$

Figure 1 shows the tree at age 5 where some substructures are not complete.

3 Photosynthesis

3.1 Introduction

The leaves produce the vegetable biomass that is distributed in the tree architecture insuring growth and organ expansions. We define an empirical function that controls the biomass production and depends on the leaf surface. We consider the biomass produced by the leaves as a pool of reserves that is shared between the organs proportionally to their sinks strength.

The sum of the product of the sinks by the corresponding organ numbers is the *total biomass attraction* sometimes called demand. The parameters of the leaf functioning and the sinks values must be estimated in order to fit a given plant architecture.

The biomass production during a cycle depends on the still alive leaves fabricated from the biomass of the previous cycles.

3.2 Organ Size Dynamic

From the formulas describing the topology of the tree we can derive the formulas giving the numbers $N_p^o(k)$ of organs on a structure of Physiological Age p and Chronological Age k which is independent of the Chronological Age of the complete tree.

$$N_p^o(0) = 0 \ , \tag{6}$$

$$N_p^o(k) = M_p^o(k, N^o) + N_p^o(k-1) \ , \qquad 0 < k < \tau_p \ , \tag{7}$$

$$N_p^o(k) = L_p^o(k, N^o) + N_{\mu(p)}(k - \tau_p) \ , \qquad \forall k \geq \tau_p \ , \tag{8}$$

with

$$M_p^o(k, N^o) = \sum_{q>p} r_{pq} \left\{ m_{pq}^o(k) + b_{pq} N_q^o(k-1) \right\} \ , \tag{9}$$

$$L_p^o(k, N^o) = \sum_{l=k-\tau_p+1}^{k} M_p^o(l, N^o) \ . \tag{10}$$

A structure $S_p(k, n)$ owns organs of different ages smaller or equal to k. The number of organs of age k are those which are born at $n - k$ that is :

$$\Delta N_p^o(n-k) = N_p^o(n-k+1) - N_p^o(n-k) \ .$$

The biomass attraction (sink) of an organ o of age k is denoted $\phi^o(k)$; it is specific to each plant and must be adjusted on real data. The total biomass attraction of the plant is then

$$D(n) = \sum_{o,p} \sum_{k=1}^{n} \phi^o(k) \Delta N_p^o(n-k) \ .$$

If the leaves a have only one physiological age, then the biomass of an organ o of physiological age p at age k produced by the photosynthesis of the leaves $Q^a(n)$ — denoted $q_p^o(k, n)$ — satisfies the fundamental Greenlab formula :

$$\boxed{q_p^o(k+1, n+1) - q_p^o(k, n) = c(n) \phi^o(k+1) \frac{Q^a(n)}{D(n+1)} \ ,} \tag{11}$$

$$q_p^o(0, n) = 0 \ ,$$

where τ_a denotes the live time of the leaves a and

$$Q^a(n) = \sum_{k=1}^{\tau_a} q^a(k, n) \Delta N^a(n-k), \quad n \geq 1, \quad Q(0) = g \ ,$$

with g the seed biomass.

To simplify, we have supposed here that the production depends linearly on the surface of the leaves and then $c(n)$ depends on the climate and the thickness of the leaves supposed to be constant here. In more general cases [3], $Q_p^a(n)$ must be substituted by a nonlinear function of $q^a(.,n)$ in the fundamental Greenlab equation.

Then, in the linear case, remarking that $\Delta N^a(n-k) = \Delta N^a(n+1-k-1)$ and multiplying (11) by $\Delta N^a(n-k)$, we see that the total biomass of the leaves $Q^a(n)$ satisfies :

$$Q^a(n+1) - Q^a(n) = \frac{c(n)\sum_{k=1}^{\tau_a} \phi^a(k)\Delta N^a(n-k+1)}{D(n+1)} Q^a(n) \, .$$

The total biomass produced being $Q(n) = c(n)Q^a(n)$ it satisfies the recurrent equation :

$$\frac{Q(n+1)}{c(n+1)} - \frac{Q(n)}{c(n)} = \frac{\sum_{k=1}^{\tau_a} \phi^a(k)\Delta N^a(n-k+1)}{D(n+1)} Q(n) \, .$$

The photosynthesis model can be formulated in term of feedback systems indeed we can write the fundamental equation (11) as

$$\begin{aligned}
q_n &= \begin{bmatrix} 0 & \cdot & \cdot & \cdot & 0 \\ 1 & 0 & \cdot & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & \cdot & 0 & 1 & 0 \end{bmatrix} q_{n-1} + \frac{1}{D(n)} \begin{bmatrix} \phi(1) \\ \cdot \\ \cdot \\ \phi(\tau_a) \end{bmatrix} u_{n-1} \, , \\
y_n &= c(n) \begin{bmatrix} \Delta N^a(n-1) & \cdot & \cdot & \cdot & \Delta N^a(n-\tau_a) \end{bmatrix} q_n \, , \\
u_n &= y_n \, ,
\end{aligned}$$

where q_n denotes the vector of the τ_a first entries of $q^a(.,n)$. Then u_n can be seen as a biomass to share between the organs and y_n the biomass generated by the photosynthesis. The feedback $u_n = y_n$ says that the biomass to share is the one generated by the photosynthesis.

3.3 Example

Forgetting the index a in the counting equations of the leaves, and supposing that there is a leave for each internode we obtain the equations :

$$\begin{aligned}
&N_p(0) = 0 \, , && p = 1,2,3 \, , \\
&N_3(k) = 1 \, , && \forall k > 1 \, , \\
&N_2(k) = 2 + 2N_3(k-1) + N_2(k-1) \, , && 3 > k > 1 \, , \\
&N_2(k) = \sum_{l=k-3}^{k-1} \{2 + 2N_3(l)\} + N_3(k-3) \, , && \forall k \geq 3 \, , \\
&N_1(k) = 3 + 2N_3(k-1) + N_2(k-1) + N_1(k-1) \, , && 5 > k > 1 \, , \\
&N_1(k) = \sum_{l=k-5}^{k-1} \{3 + 2N_3(l) + N_2(l)\} + N_2(k-5) \, , && \forall k \geq 5 \, .
\end{aligned}$$

We obtain $N_2(4) = 13$ and $N_1(9) = 5(5 + N_2(4)) + N_2(4) = 103$.

The sinks being all equal to 1, the thickness of leaves being equal to 0.05, the leaves living indefinitely, we obtain the tree of Figure 2 at age 5.

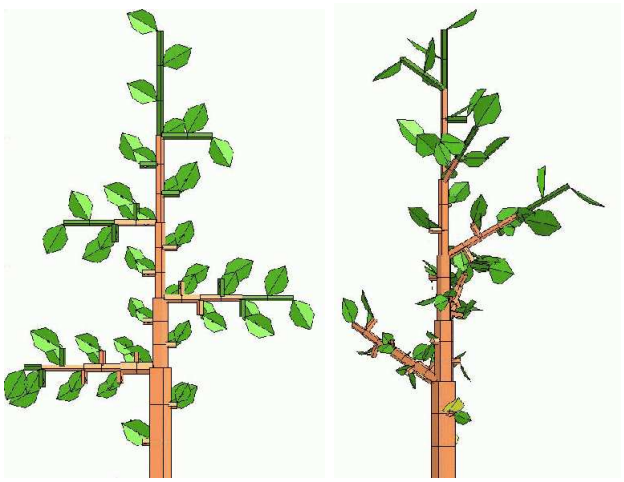

Figure 2: The correct size and geometry of the tree example at age 5.

4 Morphogenesis

To define the precise geometry of the tree we have to enrich the topological equations with the action of operators describing the phyllotaxy of the organs. For that we have first to see the substructures as a $4 \times N$ matrices of reals describing a set of N points of $\mathbb{R}^4$ (the projective space associated to $\mathbb{R}^3$) of the vertices of a triangulation of the shape of the tree. The set of these matrices is denoted $\mathcal{M}_4^*$. On this set we consider the left action by geometrical transformations represented by 4×4 matrices and the internal operation of columns concatenation represented by the operator $\oplus$. The neutral element of $\oplus$ is denoted $\mathbb{O}$ and it means the empty 4×0 matrix (the matrix of four raws with zero column).

We needs four transformations which may depend on the metamer parameters.

- The translation $\rho_{pq}(k, n)$ along z-axis in the local metamer coordinate of the length of the metamer $m_{pq}(k, n)$.
- The rotation θ_p of the branching angle around the x-axis in the local metamer coordinates.
- The rotation ψ_p of the phyllotaxy angle around the z-axis in the local metamer coordinates.

- The rotation ω_b of $2\pi/b$ around the z-axis in the local metamer coordinates corresponding to the regular repartition of the buds when appear simultaneously b buds on an internode.

Forgetting the index n in $S_p(k,n)$ which is common to all substructures, then $S_p(k) \in \mathcal{M}_4^*$ follows the recurrent equations :

$$S_p(0) = \mathbb{O}, \tag{12}$$
$$S_p(k) = R_p(k, S, S_p(k-1)), \qquad 0 < k < \tau_p\ , \tag{13}$$
$$S_p(k) = T_p(k, S, S_{\mu(p)}(k-\tau_p)), \qquad \forall k \geq \tau_p\ , \tag{14}$$

with

$$\Omega_{pq}(k,S,.)\ :\ X \in \mathcal{M}_4^* \mapsto m_{pq}(k) \oplus \rho_{pq}(k)\psi_p \left\{ \bigoplus_{i=0}^{b_p-1} \{\omega_{b_{pq}}^i \theta_p S_q(k-1)\} \oplus X \right\} \in \mathcal{M}_4^*\ ,$$

$$R_p(k,S,.) = \bigcirc_{q=p}^{P} \Omega_{pq}(k,S,.)^{\circ r_{pq}}\ ,$$

$$T_p(k,S,.) = \bigcirc_{l=k-\tau_p+1}^{k} R_p(l,S,.)\ ,$$

where we have denoted $\circ$ the composition of operators and $\bigcirc_{l=1}^{2} A(l,.)$ means $A(2,A(1,.))$.

4.1 Example

The complete tree example given in Figure 2 is obtained for a phyllotaxy of $10\pi/8$ and branching angle of $60°$.

Let us give in conclusion a more realistic tree (Figure 3) denoted $\mathcal{T}$ with 5 Physiological Ages with $\tau = (4,3,2,1,0)$, $\mu = (2,3,4,5,\bullet)$, $b_{pq} = 1$ and

$$r = \begin{bmatrix} 0 & 2 & 3 & 4 & 5 \\ 0 & 0 & 2 & 3 & 4 \\ 0 & 0 & 0 & 2 & 3 \\ 0 & 0 & 0 & 0 & 2 \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix}\ .$$

5 Conclusion

GreenLab is a dynamical model of tree growth and tree architecture, that can be written in a compact way because the botanical information is gathered at several levels of the plant organization (metamers, growth units, bearing axis, substructures). According to the needs of the application, one can count only the number of botanical organs (Organogenesis), or

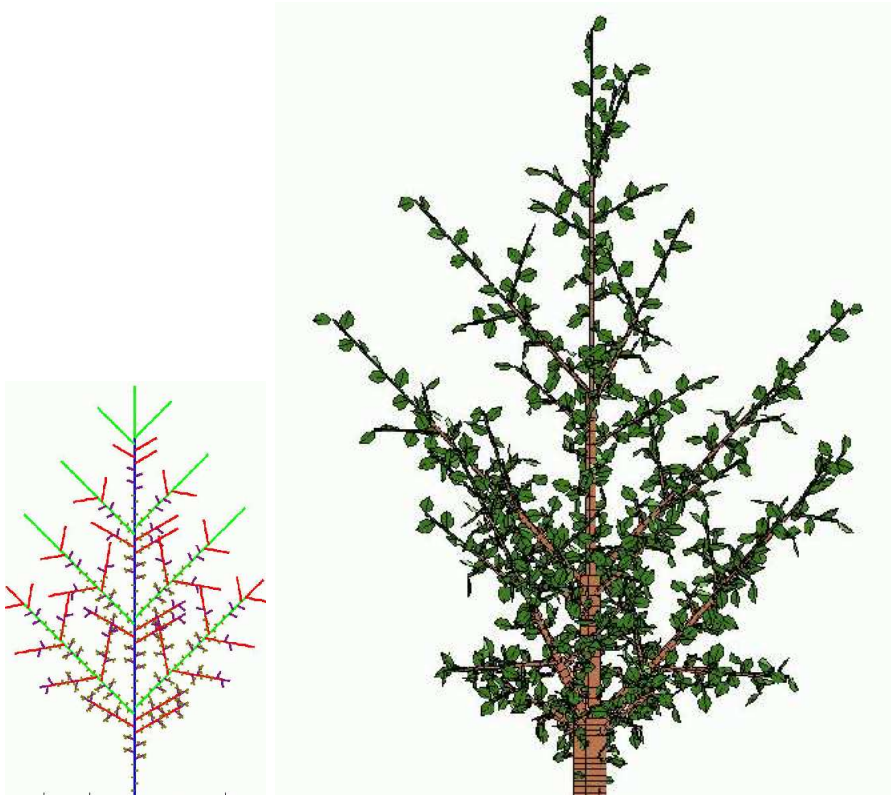

Figure 3: The geometry of $\mathcal{T}$

compute the vegetable production using a simple model of photosynthesis, or eventually determine the full plant architecture using the known botanical rules that satisfy the geometry of the plants. Each step increases the computation cost. Only the last one is costly, although the substructure method divides it dramatically compared to the usual parallel simulations of the buds functioning. In the future this new formalism should be also extended to random trees, in order to get the generating functions of the organs statistical distributions.

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